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MID-WINTER FORAGING OF COLONIES OF THE PINE PROCESSIONARY CATERPILLAR *THAUMETOPOEA PITYOCAMPA* SCHIFF. (THAUMETOPOEIDAE)

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ABSTRACT. The pine processionary caterpillar *Thaumetopoea pityocampa* Schiff. (Thaumetopoeidae) overwinters as an active larva. Field recordings made at our study site in Catalonia (Spain) during mid-winter show that the caterpillar is remarkable in its ability to locomote and feed at temperatures well below those at which the activity of most other insects is curtailed. Colonies initiated foraging bouts in the evening, 93.1 ± 35.2 minutes after the end of civil twilight and returned to the nest the following morning, 42.9 ± 24.9 minutes before the onset of civil twilight. Despite an overnight mean minimum temperature of $3.8 \pm 0.25^\circ\text{C}$ during the study period, caterpillars were active each night and did not become cold-immobilized until the temperature fell below -2°C . During the daytime, the caterpillars sequester themselves within their nests and on sunny days are able to elevate their body temperatures by conducting heat from the structures. The mean difference between the daily high and low nest temperature was $30.9 \pm 0.9^\circ\text{C}$. The maximum nest temperature recorded was 38°C . Salient features of the biology and ecology of *T. pityocampa* are compared to those of other central place foragers in an attempt to elucidate the factors that may underlie the evolution of foraging schedules in social caterpillars.

RESUMEN. La procesionaria del pino, *Thaumetopoea pityocampa* Schiff. (Thaumetopoeidae), permanece activa durante el invierno. Los registros de campo obtenidos en el presente estudio en Cataluña (España), durante la parte media del invierno, muestran que esta larva es asombrosa por su habilidad para desplazarse y alimentarse a temperaturas muy por debajo de aquellas a las que la actividad de la mayoría de los insectos es impedida. Las colonias inician su periodo de forrajeo en la noche, 93.1 ± 35.2 minutos después de la penumbra civil y regresan a sus nidos a la mañana siguiente, 42.9 ± 24.9 minutos antes del inicio de la penumbra civil. A pesar de que la temperatura mínima durante la noche en el periodo de estudio fue de $3.8 \pm 0.25^\circ\text{C}$, las larvas estuvieron activas cada noche y no se inmovilizaban por el frío hasta que la temperatura descendía por debajo de los -2°C . Durante el día, las larvas se mantenían dentro de sus nidos, dependiendo de la habilidad de estas estructuras para absorber la energía solar para elevar su temperatura corporal. En el interior de los nidos, el diferencial promedio entre la temperatura máxima y mínima fue de $30.9 \pm 0.9^\circ\text{C}$. La temperatura máxima registrada dentro de los nidos fue de 38°C . Las características sobresalientes de la biología y ecología de esta larva procesionaria son comparadas con las de otras especies de forrajeo central, en un intento por dilucidar los factores que subyacen en la evolución de los patrones de forrajeo de larvas sociales.

Additional key words: processionary behavior, trail following, activity patterns, thermal regulation.

Thaumetopoea pityocampa Schiff., the pine processionary caterpillar, is distributed throughout much of southern Europe where the larvae feed gregariously on the needles of pine (*Pinus* spp.). Colonies develop from egg masses of 70 to 300 eggs (Dajoz 2000). The siblings at first build and abandon a series of loosely spun nests but in the third instar establish a permanent nest and become central place foragers (Halperin 1990). In Catalonia (Spain), the larval stage typically extends from August until April of the following year and the caterpillars overwinter as active larvae. Although it is known that the larvae feed at night follow-

ing the establishment of their permanent nests (Fabre 1916), there have been no studies of the foraging behavior of larvae in midwinter, nor are there any long term records of foraging behavior for any time of the year. Of particular interest is the question of whether the caterpillars forage on evenings when overnight temperatures approach freezing. Of parallel interest is the role that the nest might play in enabling the caterpillars to process food in their guts at low ambient temperatures. Several investigators have made spot measurements of nest temperatures and have reported that when irradiated by the sun the structures achieve

temperatures as much as 17°C in excess of the ambient temperature (Breuer et al. 1989, Demolin 1969, Breuer & Devkota 1990, Halperin 1990), but there have been no continuous measurements of nest temperatures in midwinter. The recent availability of small, portable data loggers has made possible the uninterrupted recording of physical and behavioral data heretofore not feasible in remote locations, and a detailed database of ecologically relevant aspects of the foraging behavior of social caterpillars has begun to accumulate (Fitzgerald et al. 1989, Fitzgerald & Underwood 1998a, b, Ruf & Fiedler in press). We undertook the present study of the pine processionary caterpillar to add to this database and, more specifically, to investigate the mid-winter foraging behavior of the insect. We monitored both the daily temperature cycles of the nests and the foraging and resting cycles of the caterpillars.

MATERIALS AND METHODS

Study site. Studies of nest temperature and colony activity patterns were undertaken during February 2001 in a mountainous region near La Moixeta, (Baix Penedès County), Catalonia (Spain) (41°21'N, 001°31'E), elevation approximately 400 m. The canopy of the study area consisted almost entirely of pure stands of *Pinus halepensis* and *P. pinea*.

Climate records. Seasonal climate records for 1999–2001 were obtained from the Catalonia Meteorology Service. Data are from Font-Rubi (l'Alt Penedès County, elevation 409 m) the nearest government maintained weather station, approximately 8.5 km from the La Moixeta study site. The hot summers typical of the Mediterranean climatic zone are moderated by elevation at the La Moixeta site, and the months of November through February are correspondingly cooler with midwinter temperatures approaching, but only occasionally falling below, freezing.

Orientation of nests at the field study site. The positions of 157 *T. pityocampa* nests relative to the cardinal compass points were plotted at the study site to determine if the nests are positioned to take advantage of solar radiation. The nests occurred naturally on either *P. halepensis* or *P. pinea*. Trees were divided into quadrants each centered about a cardinal compass direction and the position of each nest on a tree assigned to one of the quadrants.

Heat gain in nests under controlled conditions. Laboratory studies were conducted to determine how nests gain and maintain heat when exposed to a radiant heat source. Four empty nests of different sizes were maintained in a temperature controlled chamber with an ambient temperature of $6.0 \pm 2.0^\circ\text{C}$ and irradiated

with a 250-W infrared lamp situated 0.5 m from the nests (Breuer & Devkota 1990, Fitzgerald & Underwood 2000). Temperature probes were inserted at the centers of the irradiated and shaded sides of the nests, approximately 2 cm below the surface. The temperature of each nest was measured at 1 minute intervals for approximately 135 minutes after which the heat source was extinguished and additional measurements made until the nests cooled to ambient temperature. Temperature measurements were automatically written to data loggers (Onset Computer Co., accuracy $\pm 0.2^\circ\text{C}$) and the data downloaded with BoxCarPro Software (Onset Computer Co.).

Temperature measurement of nests at the field study site. The internal temperatures of five nests of the pine processionary were monitored in the field from 17–26 February. Temperature probes were inserted approximately 8 cm below the upper surfaces in areas of nests occupied by caterpillars. Ambient temperatures were measured in shaded areas near the study nests. Temperature data were recorded at 15 minute intervals as described above and the data loggers downloaded at 24 h intervals. Temperature records for a total of 19 colony-days were collected.

Daily activity patterns of field colonies. Daily activity patterns of seven colonies of *T. pityocampa* occurring on different trees were monitored with infrared activity monitors (Fitzgerald & Underwood 2000) from 18–26 February. Records for a total of 26 colony-days were collected. The monitors were placed on branches bearing the major trunk trails of the colonies, approximately 20 cm from each nest. Activity monitors were connected to event loggers (Onset computer Co.) which recorded the time of day when the caterpillars triggered the monitors. A reset delay of five seconds was programmed into the recorders to minimize the probability that a single passing caterpillar would trigger the monitor more than once. Data were off loaded with BoxCarPro software at 24 hour intervals. Colonies were also observed each evening with red-filtered light and again in the early morning to aid in the interpretation of the activity recordings. In reporting the time of onset and termination of daily activity periods, we ignored isolated early starters and stragglers by considering colony activity to have started when the number of caterpillars moving past the detector reached 10 or more per 15 minutes and to have ended when the number of returning caterpillars fell to fewer than that number.

Statistical analyses. Statistical analyses as detailed below were conducted with SigmaStat and ProStat statistical software. Nest orientation was analyzed with Rayleigh's test for circular distribution (Zar 1974).

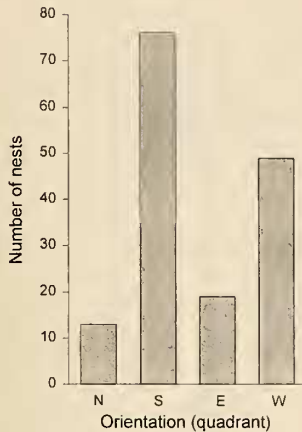


FIG. 1. Orientation of nests of *T. pityocampa* on pine trees at the study site.

RESULTS

Orientation of nests at the field study site. Approximately 61% of the nests at the study site were located within the SE-SW ($135\text{--}225^\circ$) quadrant on the crowns of trees. Nests were non-randomly distributed with a mean orientation of $204 \pm 6.8^\circ$ (SE) (Rayleigh's test of uniformity, $p < 0.01$, Fig. 1).

Heat gain in nests under controlled conditions. Empty nests exposed to a radiant heat source in the

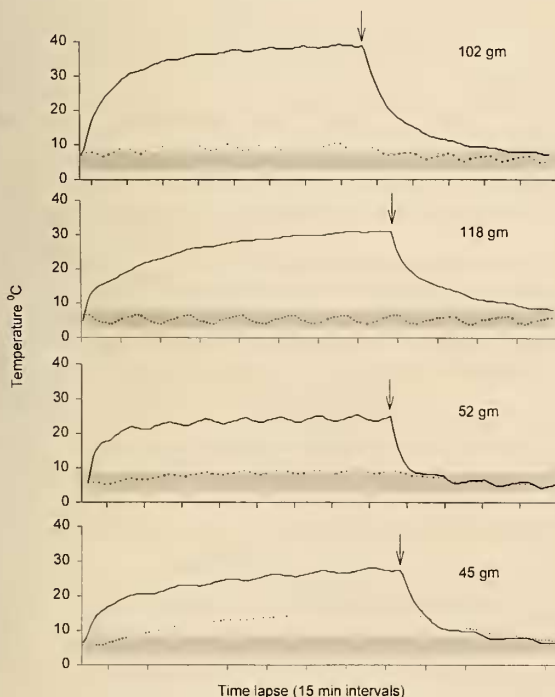


FIG. 2. Temperature within the irradiated (solid line) and shaded sides (dotted line) of four empty nests of *T. pityocampa* recorded under laboratory conditions. Ambient temperature range is indicated by the horizontal shaded bar. Arrows indicate points when artificial heat source was turned off, values indicate mass of nests.

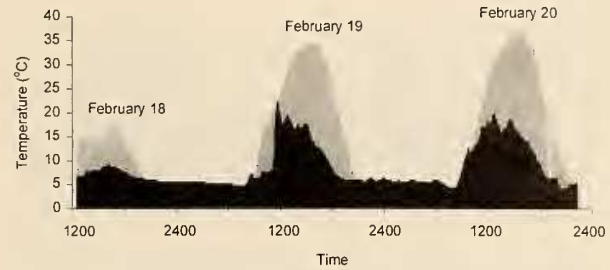


FIG. 3. Temperature inside the nest of a colony of *T. pityocampa* (gray) and ambient temperature (black) recorded over a three day period.

laboratory showed a rapid increase in internal temperature on the irradiated side (Fig. 2). The larger nests showed virtually no heat gain on the shaded sides while the shaded sides of the smaller nests had modest gains relative to the irradiated sides of the structures (Fig. 2). Temperature differentials between the irradiated and shaded sides of the nests ranged from 29.3°C in the larger nests to 13.2°C in the smaller. All of the nests cooled precipitously to ambient temperature when the heat source was removed (Fig. 2).

Diurnal fluctuation of nest temperature in the field. On 19–23 and 25 February, skies at the study site were largely cloud free. Four of our five study nests were in open areas and were directly irradiated by the sun for most of those days. The mean daily low temperature recorded in these nests was $3.8 \pm 0.25^\circ\text{C}$ and the mean daily high $34.6 \pm 1.0^\circ\text{C}$ (12 colony-days, range = $0\text{--}38^\circ\text{C}$). The mean difference between the daily high and low temperatures in the nests was $30.9 \pm 0.9^\circ\text{C}$. The mean daily high ambient temperature recorded at the study site during this period was $16.9 \pm 1.5^\circ\text{C}$. One of our study nests was in a more shaded area and experienced direct radiation for only part of the day. For this nest, the mean low temperature was $3.8 \pm 1.0^\circ\text{C}$ and the mean high $17.3 \pm 1.0^\circ\text{C}$ (4 colony-days). The mean difference between the daily high and low temperatures in the nest was $13.5 \pm 0.9^\circ\text{C}$. For all nests, daily lows occurred in the morning just before dawn and daily highs between 1200 and 1500 h. Daily temperature fluctuation recorded in one nest over a three-day period is shown in Fig. 3. Our investigations in the study area were terminated at noon on 26 February and we obtained a temperature record for the period from 2400 to 0900 h on that day. On the morning of 26 February, standing water in outdoor containers had iced over and our data loggers indicated the temperature dropped to -4°C by 0600 h, the lowest temperature recorded during the study period.

Seasonal and daily activity patterns of field colonies. A seasonal temperature profile compiled for the study area for 2000 and 2001 shows that the cater-

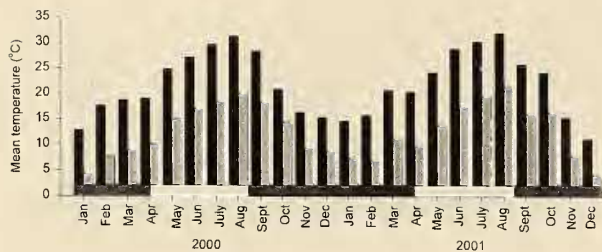


FIG. 4. Monthly mean minimum (gray) and mean maximum (black) temperatures recorded near the study site over a two year interval. Horizontal bar indicates approximate periods when *T. pityocampa* actively forages (gray) and pupates underground (white).

pillars feed and grow during the coldest part of the year and reside as pupa buried in the soil during the hot summer months (Fig. 4). Daily activity records obtained during the present study show that during the period of growth, caterpillar activity outside the nest is restricted to the coldest part of the day (Fig. 5). Despite low early morning temperatures during the study period, colonies were active overnight on all of the study days. Colonies initiated foraging bouts an average of 93.1 ± 35.2 minutes after the end of civil twilight in the evening (center of the sun 6° below horizon) and the last contingent of foragers returned to the nest 42.9 ± 24.9 minutes before the onset of civil twilight in the morning ($N = 26$ colony-days). The interval between the movement of the first contingent of caterpillars from the nest in the evening and the return of the last contingent in the morning was 618.0 ± 35.2 minutes. Thus, colonies were typically active on the tree throughout the evening and early morning hours. That colonies fed during these overnight forays was evidenced by the presence of fresh leaves in their guts after they returned to the nests. In 20 of the 26 foraging bouts recorded, colonies moved from the nest to feeding sites in the early evening and returned in the early morning, giving rise to bimodal activity patterns (Fig. 5). In the other six instances, activity between the nest and feeding sites occurred throughout the evening and early morning.

Colony activity on the two coldest nights is illustrated in Fig. 6. Overnight on 17–18 February, colonies were continually active even though temperatures measured at nest sites fell to 0°C by 2400 h. The ambient temperature was slightly below freezing at 0900 h when the whole of colony 1 was observed to still be out of the nest moving about the tree in procession. It is not known when the caterpillars returned to the nest but all were back when the nest was next observed in late afternoon. Overnight on 25–26 February the temperature fell below 0°C at approximately 2200 h and reached an overnight low of -4°C at 0600 h. Inspection of the activity record for colony 3 (Fig. 6) shows that activity was

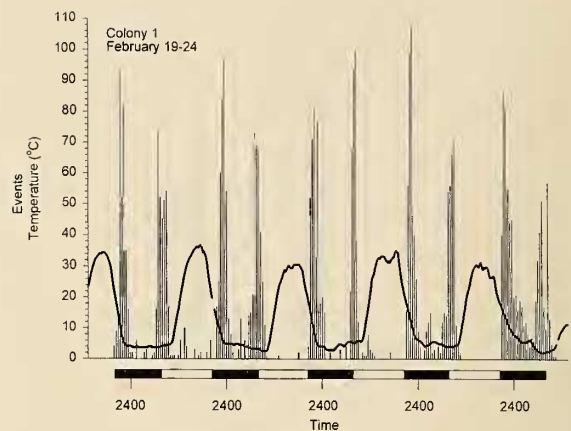


FIG. 5. Bimodal daily activity bouts of a colony of *T. pityocampa* (vertical bars) and nest temperature (black line). Horizontal bar indicates daily photoperiods (white) and scotoperiods (black). Photoperiods begin at the onset of civil twilight and end at the termination of civil twilight.

not initiated for the most part until the temperature fell below 0°C . Caterpillar activity largely ceased when the temperature reached -2°C but sporadic activity was recorded at -4°C . When this colony was observed at 0900 h on 26 February, all the caterpillars were back in the nest. The extent to which the caterpillars fed at these sub-zero temperatures is not known.

DISCUSSION

Our study, providing the first empirical data set on the temporal foraging patterns of colonies of the pine processionary, supports the observation of Fabre (1916) that the caterpillars of the pine processionary feed throughout the winter on all but the most frigid nights. The pine processionary caterpillar is remarkable in its ability to locomote and feed at temperatures well below those at which the activity of most insects is curtailed. Only a few other invertebrates are active at such low temperatures. Some collembolans (Aitchison 1983), several species of spiders (Aitchison 1984), the cricket *Grylloblatta campodeiformis* Walker (Prichard & Scholefield 1978), an amphipod (Dunbar 1957), and a copepod (Kiørboe et al. 1982) have been reported to move about and feed at temperatures at or slightly below zero. Laboratory studies of the sub-Antarctic caterpillar *Pringleophaga marioni* Viette (Tineidae) showed that the larvae are able to maintain motoric functions at temperatures as low as -1.6°C but there are no data to show that the caterpillars are active at temperatures this low in their natural environment (Klok & Chown 1997).

Locomotion and feeding in caterpillars has been recorded only rarely at temperatures below 5°C (Kevan et al. 1982, Joos 1992, Kukal 1993, Klok & Chown

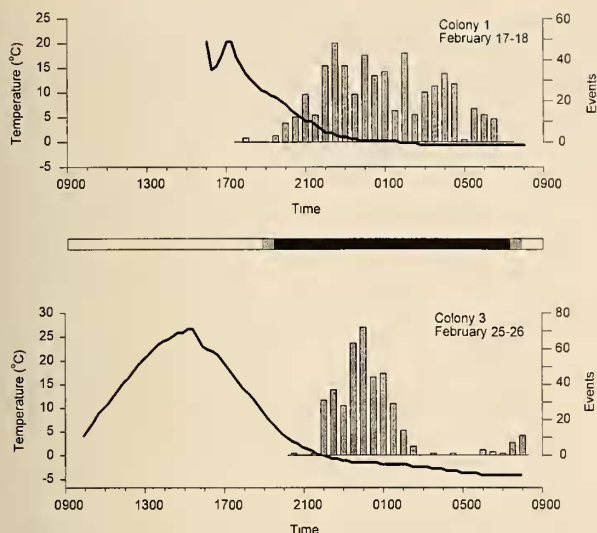


FIG. 6. Temperature in the nest (black line) and activity outside the nest (vertical event bars) of two colonies of *T. pityocampa*. Horizontal bar indicates photoperiod (white), scotoperiod (black) and civil twilight (gray).

1997). A notable exception is the social caterpillar *Eucheira socialis* Westwood (Pieridae) which feeds throughout the winter in the mountains of Mexico (Fitzgerald & Underwood 2000). The daily temperature profile in the winter in the montane forest where *E. socialis* occurs is similar to that of our study area in Catalonia in that the diurnal temperatures are moderate to warm while at night the temperatures plunge precipitously and are often near or below freezing. Like *T. pityocampa*, the caterpillars of *E. socialis* feed only at night and have been recorded outside their nests at subzero temperatures in midwinter (Fitzgerald & Underwood 2000).

Our study shows that the caterpillars of *T. pityocampa* locate their nests preferentially in the SE-SW quadrant of host trees. Brueur et al. (1989) found approximately 76% and Schwammer and Nemeschkal (1987) approximately 80% of the nests they surveyed in other areas of the Mediterranean to lie within this same quadrant. Thus, data from these studies show that colonies of the processionary locate their permanent nests on the side of the tree that is likely to receive the most solar radiation. Although fewer nests were found within this quadrant in La Moixeta, this may have been the case because the trees occurred in young stands and were distantly spaced so that they experienced little shading from nearby trees. Fitzgerald and Underwood (2000) found that the nests of *E. socialis* occurring on open grown and distantly spaced madrone trees were irradiated by the sun regardless of their position in the crown of the tree.

The ability of the inhabited nests of *T. pityocampa* to warm well above ambient temperature when irradiated was demonstrated in laboratory studies by Breuer and Devkota (1990), but our study shows that even when devoid of caterpillars the irradiated nests of *T. pityocampa* exhibit large heat gains. The overwintering nests of the processionary are densely packed with silk, frass, and host material and the bodies of the resting larvae are situated tightly within them, allowing the caterpillars to raise their T_b 's well above the temperature of the outside air by conducting heat from the structures. Although the relationship between T_b and the rate of digestion has not been determined for the processionary, nests situated on host trees to facilitate the absorption of solar radiation achieve thermal maxima during sunlit days that are likely to be well in excess of those required by the caterpillar for efficient food processing during midwinter. Data available for a few other species of caterpillars that feed at comparably low temperatures indicate that efficient food processing by the processionary is likely to require a T_b that exceeds the winter time air temperatures typical of our study site. The Arctic caterpillar *Gynaephora groenlandica* (Wöcke) (Lymanthriidae) has an assimilation efficiency of only 7% at 5°C compared to 40% at 15°C (Kukal 1993) but the assimilation threshold for *Malacosoma americanum* (Fabricius) (Lasiocampidae), which is reported to collect food at temperatures down to 7°C (Joos 1992), is not reached until the caterpillars warm to at least 15°C (Casey et al. 1988). Regardless of the thermal demands of the processionary, our study shows that the irradiated nests of the insect provide thermally heterogeneous environments (Fig. 2) within which the caterpillars might optimize their T_b 's by varying their positions within the structures during the daytime. In contrast, temperatures in shaded nests will be much cooler and may not allow optimization of T_b , placing a premium on the correct siting of the permanent nest by the third instar caterpillars. Although the caterpillars might also achieve T_b 's conducive to food processing by basking outside the nest in midwinter, the cost would be greater exposure to predators. The mean daily temperature for the coldest months (November–February) recorded at the Font Rubi station from 1999–01 was $10.7 \pm 0.7^\circ\text{C}$ and the mean daily maximum temperature for this same period was $14.7 \pm 0.5^\circ\text{C}$. Thus, if the caterpillars were to remain hidden outside the nest in protected locations during these months their T_b 's would be much lower than those achievable in the nest during this same period and might be too low to allow the efficient processing of food.

Despite the ability of the caterpillars to warm within

irradiated nests in midwinter, studies of caterpillars foraging under laboratory conditions (Fitzgerald in press) indicate that under the overall thermal regime the caterpillars experience in the field they grow at a rate well below that which they could achieve at sustained, higher temperatures. Caterpillars maintained in the laboratory at $22 \pm 2^\circ\text{C}$, under a photoperiod that simulated that experienced by field colonies of *T. pityocampa*, exhibited the same nocturnal pattern of activity as field colonies and did not feed during the day. These colonies, which eclosed from eggs in early August, completed their larval development and pupated by late October, at least 15 weeks sooner than field colonies require to complete their larval development. Halperin (1990) similarly found that the social larvae of *T. jordana* (Stgr.), which also feed during the winter, required approximately 150 days to complete their larval development in the field but only 48 days when maintained in the laboratory at a constant 25°C . The likely reason for the difference in growth rate between field and laboratory colonies of both of these species is that when maintained at elevated temperatures caterpillars are able to both collect and process food during their nocturnal forays. This allows them to assimilate more energy each day than caterpillars that experience temperatures too cold to permit food processing during the overnight foray. In addition, under field conditions, the caterpillars can be expected to assimilate little if any food on cloudy winter days.

Electronic recordings of daily foraging activity are now available for five species of social caterpillars. All are central place foragers sharing overt features of their biology (Table 1, traits 1–6). Analysis of their activity records shows that the caterpillars fall into two distinct groups based on the temporal pattern of their foraging behavior. *M. americanum* (Fitzgerald 1980, Fitzgerald et al. 1989) and *Eriogaster lanestris* (L.) (Lasiocampidae) (Ruf & Fielder in press), feed both day and night and grow rapidly, achieving their full larval growth in approximately eight weeks. *E. socialis* (Fitzgerald & Underwood 1998a), *Gloveria* sp. (Lasiocampidae) (Fitzgerald & Underwood 1998b), and *T. pityocampa* (this study) feed only at night, grow slowly, and have active larval stages lasting 7–9 months. A major constraint on caterpillars foraging is predation pressure (Stamp & Casey 1993) and for all of these caterpillars, defense against day active predators would best be served by foraging only at night and by sequestering themselves in the nest during the day. The eastern tent caterpillar, for example, has over 200 predators and parasitoids (Fitzgerald 1995), many of which might be avoided if the caterpillars hid in the nest during the daylight hours. Why then do the larvae of this species and those

TABLE 1. Comparison of traits of five species of social caterpillars. Shaded box highlights differences between species 1–2 which forage in both daylight and darkness and species 3–5 which forage only in darkness. 1 = *Malacosoma americanum*, 2 = *Eriogaster lanestris*, 3 = *Gloveria* sp., 4 = *Thaumetopoea pityocampa* and 5 = *Eucheira socialis*. See text for references.

Trait	Species				
	1	2	3	4	5
1. Central place foraging	y	y	y	y	y
2. Univoltine	y	y	y	y	y
2. Colonies average 200–300 siblings initially	y	y	y	y	y
3. Colonies construct large, silken shelters	y	y	y	y	y
4. Larvae have discrete, coordinated, bouts of en masse feeding interspersed with periods of rest	y	y	y	y	y
5. Larvae experience warm days, cool/cold nights	y	y	y	y	y
6. Caterpillars distasteful/urticating	y	y	y	y	?
7. Larvae form aposematic aggregations on the nest in daylight	y	y	n	n	n
8. Nest may overheat in sunlight causing evacuation	y	y	n	n	n
9. Rapid, progressive deterioration of host leaf quality	y	y	n	n	n
10. Larvae grow rapidly	y	y	n	n	n

of *E. lanestris* commonly rest on the outside of the nest and feed away from the structure during the daylight hours, a foraging strategy distinctly different than that of *T. pityocampa*? The answer may be sought in a suite of traits that distinguish these two species from the three nocturnal foragers (Table 1, traits 7–10). The caterpillars *M. americanum* and *E. lanestris*, both early spring feeders, are unable to feed on the aged leaves of their host trees. Their need to grow rapidly, in a race against declining food quality, may compromise safety for growth, favoring caterpillars that feed both day and night. Additionally, the nests of these species may easily overheat on hot and sunny days forcing the caterpillars to evacuate the structures and thus compromise their role as secure retreats (Joos et al. 1988, Ruf & Fiedler 2002). Both species are conspicuous against the white back ground of the nest during the day. Both are hairy and *E. lanestris* is reported to be urticating (Ruf & Fiedler in press). Both feed on species of *Prunus* whose cyanogenic glycosides may offer some defense against predators when regurgitated as cyanide (Peterson 1987, Fitzgerald et al. 2002). Thus, aposematism and distastefulness may offset the risk of daytime exposure to some extent.

More enigmatic is the fact that the colonies of *E. socialis*, *Gloveria* sp., and *T. pityocampa* feed only nocturnally and do not take advantage of the warm daylight hours to collect additional food. Although it is not known if *E. socialis* is distasteful to predators, *Gloveria*

sp. and particularly the older instars of *T. pityocampa* are urticating (Vega et al. 1999), and it would appear that they would be as well or better defended than *M. americanum* or *E. lanestris* were they to feed in the daytime. Perhaps most significant is the fact that these three nocturnally active species feed non-selectively on the leaves of their host trees and have no pressing need to accelerate their rates of feeding to keep pace with a seasonal decline in host quality. Furthermore, the nests of these species are denser and more opaque to radiation than those of *M. americanum* and *E. lanestris* and there is no evidence that the whole of these structures can become uninhabitable due to overheating. They therefore constitute dependable daytime retreats from predators. Thus, as may be the case for *M. americanum* and *E. lanestris*, none of these species needs to compromise safety for growth.

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LITERATURE CITED

- AITCHISON, C. W. 1983. Low temperature and preferred feeding by winter-active collembolans. *Pedobiologia* 25:27–36.
- . 1984. Low temperature feeding by winter-active spiders. *J. Arachnol.* 12:297–305.
- BREUER, M. & B. DEVKOTA. 1990. Studies on the importance of nest temperature of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Thaumetopoeidae). *J. Appl. Entomol.* 109:331–335.
- BREUER, M., B. DEVKOTA, E. DOUMA-PETRIDOU, A. KOUTSAFTIKIS & G. H. SCHMIDT. 1989. Study on the exposition and temperature of nests of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Thaumetopoeidae) in Greece. *J. Appl. Entomol.* 107:370–375.
- CASEY, T. M., B. JOOS, T. D. FITZGERALD, M. YURLONA & P. YOUNG. 1988. Group foraging, thermoregulation, and growth of eastern tent caterpillars in relation to microclimate. *Physiol. Zool.* 61:372–377.
- DAJOZ, R. 2000. Insects and forests. The role and diversity of insects in the forest environment. Lavoisier Publishing, Paris.
- DEMOLIN, G. 1969. Bioécologie de la processionnaire du pino, *Thaumetopoea pityocampa* Schiff. Incidencia de los factores climáticos. *Bol. Serv. Plagas Forest* 12:9–22.
- DUNBAR, M. J. 1957. The determinants of production in northern seas: a study of the biology of *Themisto libellula* Mandt., "Calanus" Series no. 14. *Can. J. Zool.* 35:797–819.
- FABRE, J. H. 1916. The life of the caterpillar. Dodd, Mead and Co. Inc., New York.
- FITZGERALD, T. D. 1980. An analysis of daily foraging patterns of laboratory colonies of the eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae), recorded photoelectronically. *Can. Ent.* 112:731–738.
- . 1995. The tent caterpillars. Cornell University Press, Ithaca, New York.
- . In press. The role of a trail pheromone in the foraging and processionary behavior of *Thaumetopoea pityocampa*. *J. Chem. Ecol.*
- FITZGERALD, T. D., T. M. CASEY & B. JOOS. 1989. Daily foraging schedule of field colonies of the eastern tent caterpillar *Malacosoma americanum*. *Oecologia* 76:574–578.
- FITZGERALD, T. D., P. M. JEFFERS & D. MANTELLA. 2002. Depletion of host derived cyanide in the gut of the eastern tent caterpillar, *Malacosoma americanum*. *J. Chem. Ecol.* 28:257–268.
- FITZGERALD, T. D. & D. L. A. UNDERWOOD. 1998a. Trail marking by the larva of the Madrone butterfly *Eucheira socialis* and the role of the trail pheromone in communal foraging behavior. *J. Insect Behav.* 11:247–263.
- . 1998b. Communal foraging behavior and recruitment communication in *Gloveria* sp. (Lepidoptera: Lasiocampidae). *J. Chem. Ecol.* 24:1381–1396.
- . 2000. Winter foraging patterns and voluntary hypothermia in the social caterpillar *Eucheira socialis*. *Ecol. Entomol.* 25:1–10.
- HALPERIN, J. 1990. Life history of *Thaumetopoea* spp. (Lep., Thaumetopoeidae) in Israel. *J. Appl. Entomol.* 110:1–6.
- JOOS, B. 1992. Adaptations for locomotion at low body temperatures in eastern tent caterpillars, *Malacosoma americanum*. *Physiol. Zool.* 65:1148–1161.
- JOOS, B., T. M. CASEY & T. D. FITZGERALD. 1988. Roles of the tent in behavioral thermoregulation of eastern tent caterpillars. *Ecology* 69:2004–2011.
- KEVAN, P. G., T. S. JENSEN & J. D. SHORTHOUSE. 1982. Body temperatures and behavioral thermoregulation of high Arctic woolly-bear caterpillars and pupae (*Gynaephora rossii*, Lymantriidae: Lepidoptera) and the importance of sunshine. *Arctic and Alpine Research* 14:125–136.
- KJØRBOE, T., F. MØHLENBERG & H. NICOLAISEN. 1982. Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Lilljeborg) in relation to food consumption and temperature. *Ophelia* 21:181–194.
- KLOK, C. J. & S. L. CHOWN. 1997. Critical thermal limits, temperature tolerance and water balance of a sub-Antarctic caterpillar, *Pringleophora marioni* (Lepidoptera: Tineidae). *J. Insect Physiol.* 43:685–694.
- KUKAL, O. 1993. Biotic and abiotic constraints on foraging of arctic caterpillars, pp. 509–522. In Stamp, N. E. & Casey, T. M. (eds.), *Caterpillars: ecological and evolutionary constraints on foraging*. Chapman and Hall, New York.
- PETERSON, S. C., N. D. JOHNSON & J. L. LEGUYADER. 1987. Defensive regurgitation of allelochemicals derived from host cyanogenesis by eastern tent caterpillars. *Ecology* 68:1268–1272.
- PRITCHARD, G. & P. SCHOLEFIELD. 1978. Observations on the food, feeding behavior, and associated sense organs of *Grylloblatta campodeiformis* (Grylloblattodea). *Can. Entomol.* 110:205–212.
- RUF, C. & K. FIEDLER. 2002. Tent-based thermoregulation in social caterpillars of *Eriogaster lanestris* (Lepidoptera: Lasiocampidae): behavioral mechanisms and physical features of the tent. *J. Thermal Biol.* 27:493–501.
- . In press. Plasticity in foraging patterns of colonies of the small egggar moth, *Eriogaster lanestris* (Lepidoptera: Lasiocampidae). *Oecologia*.
- SCHWAMMER, H. & H. L. NEMESGHKAL. 1987. Bedeutung der Exposition von Raupen-Nestern Pinienprozessionsspinner (*Thaumetopoea pityocampa* Schiff.) auf der Insel Krk, Dalmat. *Verh. Dtsch. Zool. Ges.* 80:298.
- STAMP, N. E. & T. M. CASEY. 1993. *Caterpillars: ecological and evolutionary constraints on foraging*. Chapman and Hall, New York.
- VEGA, J. M., I. MONEO, A. ARMENTIA, J. FERNÁNDEZ, J. VEGA, R. DE LA FUENTE, P. SÁNCHEZ & E. SÁNGHIS. 1999. Allergy to the pine processionary caterpillar (*Thaumetopoea pityocampa*). *Clinical and Experimental Allergy* 29:1418–1423.
- ZAR, J. 1974. *Biostatistical analysis*. Prentice Hall, Inc. Englewood Cliffs, New Jersey.